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Effects of Intraspecific Density and Environmental Variables on Electrofishing Catchability of Brown and Rainbow Trout in the Colorado River

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Abstract.—We investigated electrofishing catchability (q) for brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* in the Colorado River, Grand Canyon National Park, Arizona, over a range of fish densities, water temperatures, turbidities, conductivities, shoreline types, and seasons. The covariance of q with rainbow trout density strongly resembled random distributions, thereby suggesting no relationship between q and rainbow trout density. The catchability of rainbow trout was greater in turbid water (≥480 nephelometric turbidity units [NTU]) than in clear water (≤10 NTU), although lower water temperature may have contributed to this effect. The catchability of rainbow trout was greatest over sand–silt shorelines. The catchability of brown trout increased sharply to levels above those predicted from random chance up to about 0.025 fish/m^2 and then assumed an asymptotic or declining relationship with intraspecific fish density. In contrast to the situation with rainbow trout, the catchability of brown trout was higher over rocky shorelines (cobbles, boulders, and bedrock) than sand–silt shorelines, suggesting that the variability of q in relation to shoreline type is species specific. We hypothesize that the catchability of rainbow trout is influenced more by environmental variables than by density. We also hypothesize that brown trout catchability varies with density because a greater proportion of fish occur in shallow, nearshore areas (where electrofishing is most effective) when fish density is high. This effect is enhanced by high catchability over rocky substrates. Our findings emphasize the need to understand the biological and environmental factors affecting electrofishing catchability, especially in monitoring programs that rely on catch-per-unit-effort data to accurately represent fish population status and trends.

Catchability (q) is the proportion of a fish population removed by one unit of fishing effort (Peterman and Steer 1981; Hilborn and Walters 1992; McInery and Cross 2000; Bayley and Austen 2002). Correction of catch-per-unit-effort (CPUE) data for variation in catchability caused by sampling procedures, fish behavior, and environmental conditions can facilitate unbiased comparisons of fish populations across aquatic systems (Bayley and Austen 2002). For a given type of fishing equipment, catchability varies among fish species and body size (Bayley and Austen 2002), fish density (Peterman and Steer 1981; McInery and Cross 2000), and environmental variables such as water temperature, conductivity, and turbidity (Danzmann et al. 1991; Hill and Willis 1994; McInery and Cross 2000). Catchability may also vary with fish behavior among diel and seasonal sampling periods (Cross and Stott 1975; Peterson and Cederholm 1984; Dumont and Dennis 1997; Pierce 1997) and among instream habitat features (Bohlin 1977; Bohlin and Sundstrom 1977).

Electrofishing catchability often varies inversely with fish density (McInery and Degan 1993; McInery and Cross 2000; Bayley and Austen 2002). Using whole-lake electrofishing data, McInery and Cross (2000) demonstrated that gear saturation explained the negative relationship between q and largemouth bass *Micropterus salmo-*

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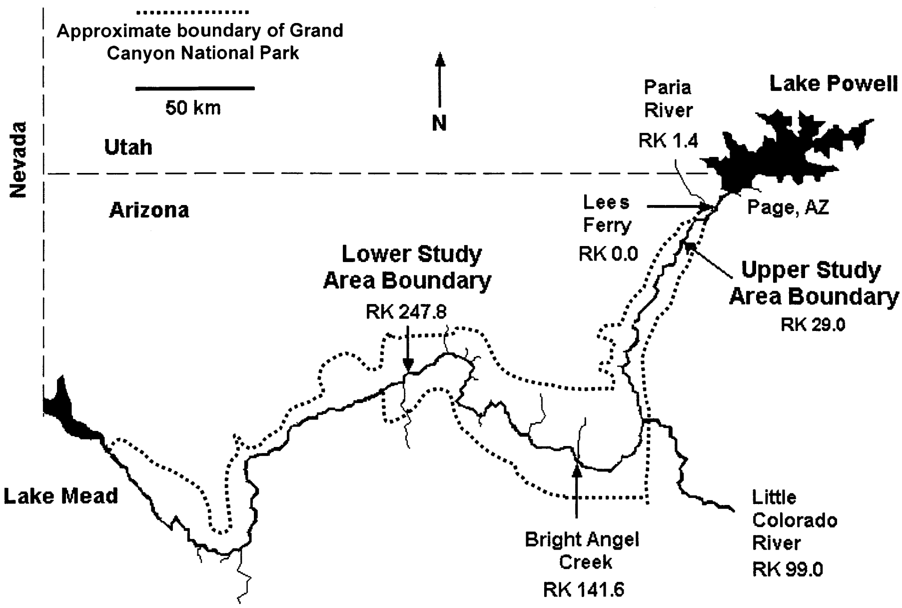

FIGURE 1.—Study area sampled during June 2000–March 2001 on the Colorado River in Grand Canyon National Park, Arizona. All locations shown are in river kilometers (RK) below Lees Ferry (RK 0.0).

ides density, although the effects of density were ameliorated by water clarity and temperature. Bayley and Austen (2002) found that for several species of fish, gear saturation occurred in areas of high fish density, particularly for DC electrofishing. In contrast, other authors observed no relationships between catchability and fish density. Hill and Willis (1994) noted no relationship between *q* and density for DC electrofishing, although they found a negative relationship for AC electrofishing. Coble (1992) and Edwards et al. (1997) found no relationship between electrofishing catchability and fish density for a Wisconsin lake and Texas ponds, respectively.

Physical factors often influence electrofishing catchability indirectly through the response of fish to heterogeneity of instream habitats (Bohlin and Sundstrom 1977). Bohlin (1977) and Dewey (1992) found that instream cover and water clarity, respectively, influenced electrofishing catchability by affecting the ability of netters to catch stunned fish. Electrofishing is inefficient at extremely high conductivities (1,000–3000 μS/cm; Reynolds 1996), and Serns (1982) and Bayley and Austen (2002) reported no significant effects of conductivity less than 1500 μS/cm on catchability. Dumont and Dennis (1997) also found no relationship between conductivity and electrofishing efficiency, and concluded that interactions between seasonal effects and light intensity (resulting from high turbidity or diel sample periods) explained much variation in electrofishing catch rates. McInery and Cross (2000) noted significant effects of water clarity, conductivity, and temperature on electrofishing catch rates, but also maintained that density-dependent effects on catchability were equally important in interpreting catch rate data.

Our objective was to determine if the seasonal catchability of rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* was related to fish density, turbidity, conductivity, water temperature, shoreline types, or substrate characteristics in the Colorado River, Grand Canyon National Park, Arizona. Since the mid-1980s, electrofishing from boats has been an important means of data collection in monitoring programs for Colorado River sport fish populations (Sharber et al. 1994; McKinney et al. 2001) and, to a lesser extent, native fish communities (Valdez and Ryel 1995). However, little is known of the factors affecting catchability of salmonids in the Colorado River and in large rivers in general.

Methods

Study area.—All locations in this study are referred to in river kilometers (RK) below Lees Ferry (Coconino County, north-central Arizona; RK 0.0) in the Glen Canyon National Recreation Area (Figure 1). Studies were conducted between RK 29.0 (Marble Canyon) and RK 247.8 (Middle Granite

TABLE 1.—Sample periods (trip dates), number of depletion trials, locations (river kilometers [RK] below Lees Ferry), and sample sizes among shoreline types in the Colorado River, Grand Canyon National Park, Arizona, during June 2000–March 2001 (SS = sand–silt shoreline types, i.e., debris fans, sand bars, and talus slopes; RS = rocky shoreline types, i.e., ledges, cliff faces, and bedrock).

Trip dates	Number of depletion trials	RK sampled	Number of shoreline types sampled
Jun 4–18, 2000	13	35.8–141.5	SS:8 RS:5
Jul 21–Aug 3, 2000	28	59.1–249.3	SS:17 RS:11
Aug 25–Sep 6, 2000	15	29.6–119.4	SS:11 RS:4
Dec 13, 2000–Jan 1, 2001	3	141.6–156.9	SS:2 RS:1
Mar 9–18, 2001	13	132.1–141.6	SS:10 RS:3

Gorge) of the Colorado River in the Grand Canyon. River morphology is strongly governed by the geology of specific stream reaches (Schmidt and Graf 1990; Converse et al. 1998). In general, the river ranges in character from numerous large eddy complexes in depositional reaches to narrow, deeply incised sections in reaches composed of resistant rock types.

Hypolimnetic water discharged from Glen Canyon Dam near Page, Arizona (Figure 1), strongly influences the hydrology and water quality of the Colorado River in the Grand Canyon. Water discharged from Glen Canyon Dam is typically clear (<5 nephelometric turbidity units [NTU]; N. Hornewer, U.S. Geological Survey [USGS], unpublished data), cold (8–11°C; Stanford and Ward 1991), and of intermediate conductivity (700–900 μS/cm; R. Hart, USGS, unpublished data). Water temperature increases linearly with distance below the dam at a rate of about 0.02°C/RK during summer months (Converse et al. 1998). Turbidity of the Colorado River can rise to over 3,000 NTU (N. Hornewer, USGS, unpublished data) during spring and late summer flooding when discharge and sediment inputs from the Paria River (RK 1.4), the Little Colorado River (RK 99.0), and numerous side canyons increase dramatically.

Nonnative rainbow and brown trout are among the most common fish species found in the Colorado River in the Grand Canyon. Rainbow trout are most abundant from Glen Canyon Dam to RK 100, whereas maximum brown trout density occurs near Bright Angel Creek (RK 142; Valdez and Ryel 1995; Valdez et al. 2001). Flannelmouth sucker *Catostomus latipinnis*, bluehead sucker *C. discobolus*, humpback chub *Gila cypha*, and speckled dace *Rhinichthys osculus* are native species that occur throughout the river, as do a host of nonnative, cyprinid fishes (Holden and Stalnaker 1975; Hoffnagle et al. 1999).

Sampling methods.—We electrofished on four river trips during 2000 and in March 2001 (Table 1). We used two, 16-ft inflatable boats outfitted for electrofishing, using a Coffelt Mk XXIV CPS unit to apply a complex pattern of pulsed DC (310 V, 15 A; Sharber et al. 1994) to a 35-cm spherical electrode. On each sampling occasion, we began data collection at dusk and concluded at midnight or shortly thereafter. The same two drivers operated boats on 60 of 72 total samples. Netting crews consisted of two persons per boat, at least one of whom participated in all five trips. We counted and measured all captured fish (maximum total length, mm) and recorded all electrofishing effort.

We estimated catchability by conducting rapid depletion trials in discrete areas (Zippin 1956; Ricker 1975; Hilborn and Walters 1992). We selected transects for depletion trials according to the availability of shoreline features that minimized immigration and emigration between electrofishing passes. Sandbars at the lower ends of eddy complexes provided the best barrier to immigration and emigration because such areas were almost always devoid of trout. Debris fans, rapids, and rock outcrops also served as barriers. We selected large eddy complexes for about half of the trials because they always contained shoreline barriers. Most of the 67 transects in the study were sampled only once, although two were sampled several times on separate trips as part of another study.

Each depletion trial was conducted over a period of 1–2 h each night. Based on results from initial depletion samples, we assumed that the short amount of time between trials minimized immigration and emigration. We electrofished transects repeatedly until the catch was reduced to about 20% of the catch from the initial pass. We processed fish between passes and retained them in a mesh live well until each experiment was concluded.

Mean transect length (estimated from aerial photographs) was 195 m and ranged from 80 to 338 m. During March 2001, netters visually estimated mean transect width (i.e., linear distance between boat and shoreline) several times during each run. Netters used reference marks at 1-m intervals on net handles to estimate transect width. Estimated average transect area for the entire study was 809 m^2 and ranged from 332 to 1736 m^2.

Data analysis.—We estimated fish abundance in electrofishing transects through maximizing the following binomial log likelihood for numbers of fish captured during individual depletion passes (Zippin 1956; Ricker 1975; Hilborn and Walters 1992):

$$P(C_i \mid N_i, q) = \log_e\{N_i!/[C_i!(N_i - C_i)!]q^{C_i}(1 - q)^{N_i - C_i}\}. \quad (1)$$

where C_i is the number of fish captured during the ith pass, and N_i is the number of fish present at the beginning of the ith pass. For each sample, we computed likelihoods directly using equation (1) over a range of integer values for N_1 (number of fish in the electrofishing transect prior to sampling) until a maximum likelihood was identified. Catchability q (the sum of fish captured over all passes divided by the sum of fish remaining prior to each pass) was computed at the conditional likelihood estimate maximized by N_1.

To evaluate species-specific covariance of catchability with fish abundance, we compared plots of observed q in relation to N_1 to pairs generated by random chance through a Monte Carlo procedure. In these simulations we utilized the same likelihood function (1) for simulations that we used for analysis of field data. We simulated 100 four-pass depletion trials in which true catchability was set to the mean catchability from field data (0.22 for brown trout, 0.56 for rainbow trout). We varied true N_1 across the range of density estimated from field data (0.025–0.075 fish/m^2 for brown trout, and 0.025–0.175 fish/m^2 for rainbow trout). Catches for each simulated depletion pass i were generated randomly from a binomial distribution given q and deducted from N_i, the expected number of fish in the site prior to the pass. Combinations of apparent catchability (q') and initial abundance (N_1') that maximized the likelihood for each simulated depletion trial thus represent covariance of the parameters due to random chance. We overlaid plots of q and N_1 (observed covariance of parameters) on those of q' and N_1' (expected covariance of parameters due to random chance) and inspected them for differences.

Abiotic characteristics of depletion transects consisted of shoreline and substrate type (categorical data) and turbidity, water temperature, and conductivity (continuous data). We classified electrofishing transects according to definitions described by Converse et al. (1998), which included bedrock (ledges and cliffs), cobble bars, debris fans (partially embedded boulders deposited at the mouths of side canyons), sand bars, and talus (boulders deposited by rockfalls). We ranked substrate type (0–10) according to a modified Wentworth scale (0 = clay/silt, 10 = bedrock; Wentworth 1922).

Due to the nonrandom selection of electrofishing depletion transects, about half of the variable levels for shoreline and substrate type contained five samples or less. To help overcome the inflated variance from small sample sizes, we created a third variable that combined substrate type rankings and shoreline type designations. We did this by conducting a correspondence analysis (Phillips 1995), a chi-square-based data reduction technique that identifies associations between the classification levels of the two variables (shoreline and substrate types). Association between levels of substrate and shoreline type was significant ($\chi^2 = 87.4$, df = 63, $P = 0.02$). Groups of variable levels resulting from the analysis consisted of rocky shorelines (>100-mm particles, including ledges, cliff faces, bedrock, and cobble bars) and sand–silt shorelines (debris fans, sand bars, and talus slopes; Table 1). The inclusion of talus slopes with finer substrates is due to our selection of large eddy complexes for depletion experiments. In such areas, shorelines were commonly comprised of talus, but substrates also contained large percentages of sand due to deposition by recirculation flows. Rocky shorelines, by contrast, were not necessarily associated with eddies and rarely contained large amounts of sand.

Turbidity and conductivity (N. Hornewer and R. Hart, USGS, unpublished data) were measured by automated datasondes deployed above the mouth of the Little Colorado River (RK 99.0) and near Bright Angel Creek (RK 141.6). An automated gauge at RK 0.0 recorded river discharge (U.S.

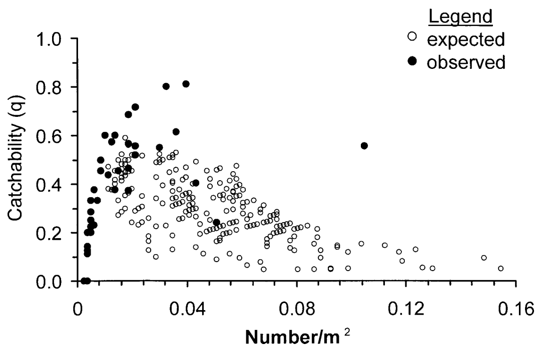

FIGURE 2.—Catchability of brown trout in relation to estimated fish density (fish/m^2) in the Colorado River, Grand Canyon National Park, Arizona, during June 2000–March 2001. Solid circles are estimates from depletion trials and open circles represent expected values due to random chance for 0.025, 0.050, and 0.075 fish/m^2.

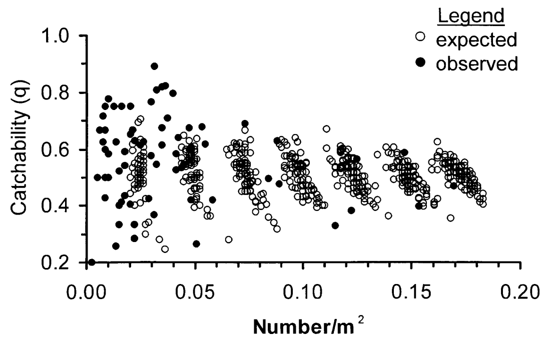

FIGURE 3.—Catchability of rainbow trout in relation to estimated fish density (fish/m^2) in the Colorado River, Grand Canyon National Park, Arizona, during June 2000–March 2001. Solid circles are estimates from depletion trials and open circles represent expected values due to random chance for 0.020–0.175 fish/m^2.

Geological Survey 2002). We recorded water temperature once per day immediately prior to sampling. We evaluated seasonal changes in turbidity, conductivity, and temperature through a one-way analysis of variance (ANOVA) and used Tukey's honestly significant difference (HSD) test to identify differences among means.

For each species, we examined relationships between seasonal and environmental variables and catchability coefficients simultaneously by analysis of covariance (ANCOVA). We treated shoreline type and sampling occasion as fixed and random factors, respectively, and temperature, turbidity, and conductivity as covariates. Catchability coefficients for rainbow trout strongly approximated normality, whereas those for brown trout were skewed to the left and transformed to their arcsine values for analysis (Sokal and Rohlf 1973). We considered all effects significant at α equal to 0.20 (Hardin and Connor 1992), which increased the power of the ANCOVA to 0.62–0.79 for the detection of moderate effect sizes (Cohen 1988). Additionally, α equal to 0.20 allowed more equitable probabilities of type I and type II errors than lower α values (Peterman 1990). To identify specific relationships between independent variables and catchability, we conducted posthoc comparisons of means using the Tukey HSD test after a one-way ANOVA for categorical effects (shoreline type, sampling occasion) and Pearson correlations for covariates.

Results

Length distributions for both species were bimodal, although 80% and 71% of rainbow and brown trout, respectively, were between 250 and 400 mm. Mean q for brown trout was 0.22 (SD = 0.22) and ranged from 0 to 0.81. Monte Carlo simulations (with q set at 0.22) indicated that due to random chance, q' declined with increasing N_1' within and across simulations of 0.025, 0.050, and 0.075 fish/m^2 (Figure 2). Brown trout q estimates from depletion trials sharply increased with N_1 from 0 to 0.025 fish/m^2 to levels above those predicted by random chance. Mean q for rainbow trout was 0.56 (SD = 0.16) and ranged from 0 to 0.88. Monte Carlo simulations indicated that, assuming $q = 0.56$, q' varied inversely with N_1' within individual simulations, but did not vary across simulations (Figure 3). Similarly, q from depletion trials did not vary with N_1.

During June–August 2000, discharge from Glen Canyon Dam was stable at 233 m^3/s. Diel discharge fluctuated from 267 to 482 m^3/s during December 2000, and ranged from 259 to 487 m^3/s during March 2001. Mean water temperature was stable at about 15°C during June–July 2000, then declined throughout the remainder of the study period to about 9.5°C ($F = 94.8$, df = 4, $P < 0.001$; Figure 4, top). Turbidity was low during June, July, and December of 2000 but increased by two orders of magnitude below the Little Colorado River during August 2000 and March 2001 ($F = 40.8$, df = 4, $P < 0.001$; Figure 4, middle). Conductivity varied little throughout the study period (ca. 780–880 μS/cm), but was higher during December 2000 and March 2001 than the preceding seasons ($F = 1.8$, df = 4, $P = 0.141$; Figure 4, bottom).

Catchability of brown trout varied between

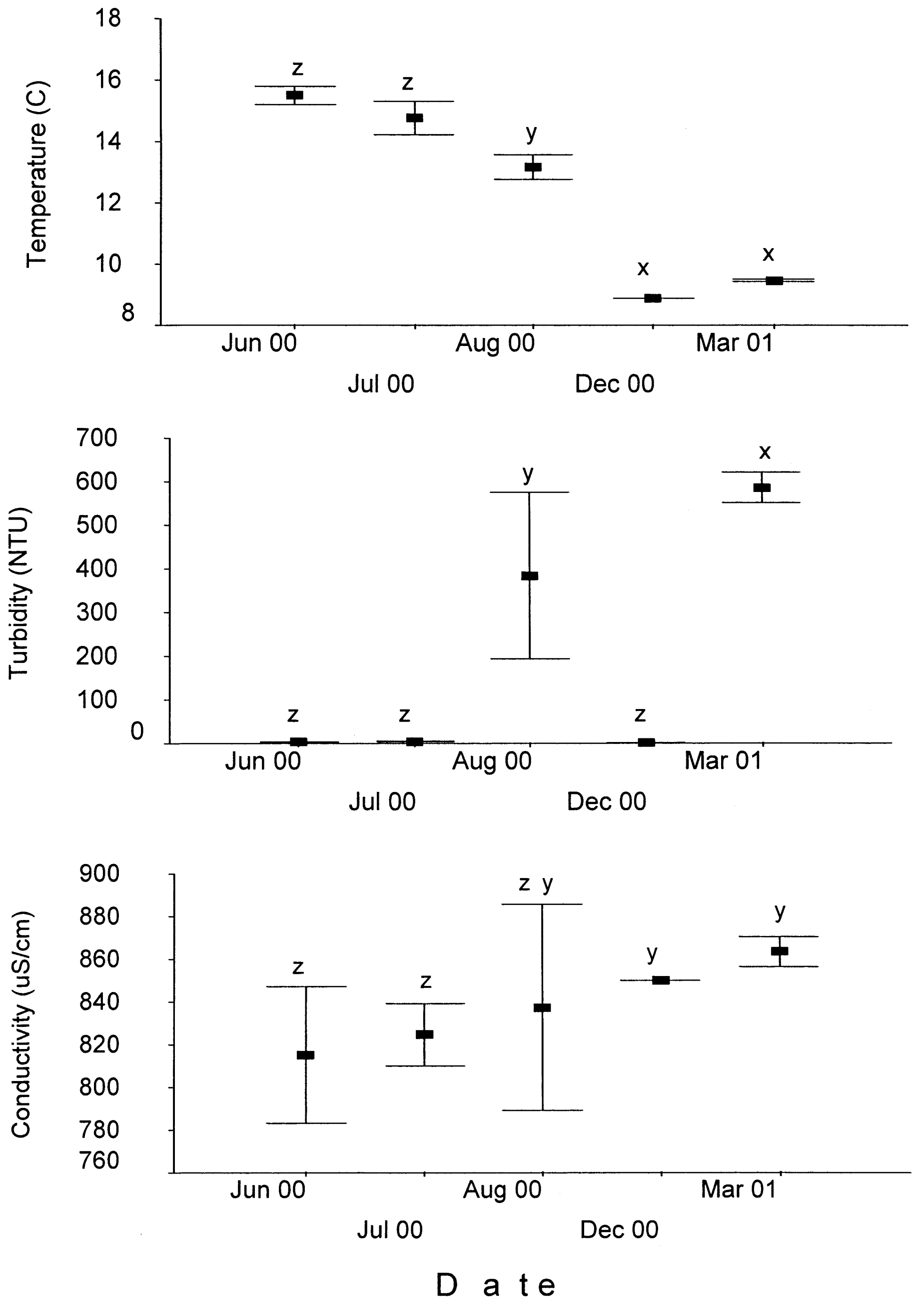

FIGURE 4.—Mean water temperature (°C), turbidity (nephelometric turbidity units [NTU]), and conductivity (μS/cm) among sampling occasions in the Colorado River, Grand Canyon National Park, Arizona, during June 2000–March 2001. The temperature data shown are averages from all sample locations, whereas turbidity and conductivity are averages from the gauges at RK 99.0 and 141.6. Vertical bars show 95% confidence intervals. Identical letters above error bars indicate no significant difference between means (α = 0.20).

TABLE 2.—Analysis of covariance for rainbow and brown trout catchability coefficients in relation to temperature, turbidity, conductivity, shoreline type (SH), and sampling occasion (SO) in the Colorado River, Grand Canyon National Park, Arizona, during June 2000–March 2001.

Species	Source of variation	df	*F*	*P*
Rainbow trout	Temperature	1	1.08	0.30
	Turbidity	1	4.97	0.03
	Conductivity	1	2.53	0.12
	SH	1	2.16	0.18
	SO	4	3.83	0.05
	SO × SH	4	0.93	0.45
Brown trout	Temperature	1	1.24	0.27
	Turbidity	1	0.02	0.89
	Conductivity	1	0.24	0.63
	SH	1	3.79	0.09
	SO	4	2.83	0.11
	SO × SH	4	1.21	0.32

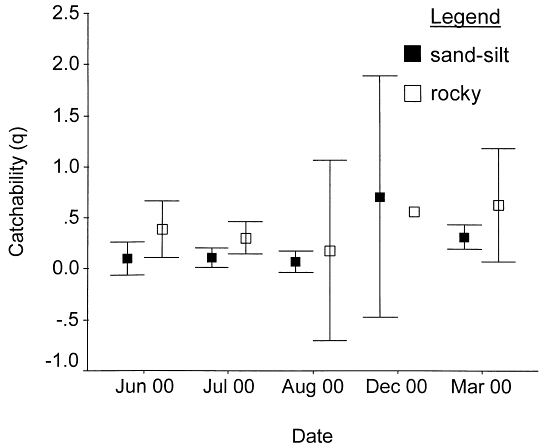

FIGURE 5.—Catchability coefficients of brown trout among sampling occasions and shoreline types (solid squares = sand–silt shorelines, i.e., debris fans, sand bars, and talus slopes; open squares = rocky shoreline types, i.e., ledges, cliff faces, bedrock, and cobble bars) in the Colorado River, Grand Canyon National Park, Arizona, during June 2000–March 2001. Vertical bars show 95% confidence intervals.

shoreline types and among sampling occasions (Table 2), and variability between shoreline types was consistent among sampling occasions. Brown trout catchability was 2.3 times higher along rocky shorelines than along sand–silt shorelines ($F = 12.2$, df = 1, $P = 0.001$; Figure 5) and was greater during December 2000 and March 2001 ($F = 7.1$, df = 4, $P < 0.001$; Table 3) than previous sampling occasions, which were not statistically different from one another.

Catchability of rainbow trout varied among sampling occasions, between shoreline types, and with turbidity and conductivity (Table 2). Variability between shoreline types was consistent among sampling periods. Catchability was 22% greater over sand–silt than rocky shoreline types ($F = 7.1$, df = 1, $P = 0.009$). Catchability increased from July to August 2000 and remained at that level through March 2001 ($F = 6.5$, df = 4, $P < 0.001$; Table 3). Rainbow trout catchability was positively related to turbidity ($r = 0.30$, N = 72, $P = 0.005$) and was 21% greater at or above 480 NTU than at lower levels (Figure 6). Conductivity was not significantly related to catchability in the absence of other variables.

Discussion

For both rainbow and brown trout, we assumed that the effect of fish size on catchability was minimal because most fish captured fell within a single length mode. However, variance of catchability was species-specific and attributable to a host of biotic and abiotic factors. We hypothesize that as brown trout density increased from zero to 0.025 fish/m^2, their spatial distribution changed such that a higher proportion of N_1 occurred in shallow, nearshore areas (where electrofishing is most effective) than at lower fish density. The positive relationship between brown trout q and N_1 is unusual in that it directly contradicts the more typical inverse relationship intrinsic to the binomial estimation procedure at low fish density. The left-hand side of the curve resembles a type III predator–prey relationship (Holling 1959) as adapted for catchability by Peterman and Steer (1981). In a type III curve, catchability is initially

TABLE 3.—Species-specific mean catchability for each sampling occasion during June 2000–March 2001 in the Colorado River, Grand Canyon National Park, Arizona. Means followed by identical letters are not significantly different at $\alpha = 0.20$.

	Sampling occasion				
Species	Jun 2000	Jul 2000	Aug 2000	Dec 2000	Mar 2001
Rainbow trout	0.54 zyw	0.48 z	0.61 wx	0.67 yx	0.71 x
Brown trout	0.21 zx	0.18 z	0.09 z	0.66 yx	0.38 x

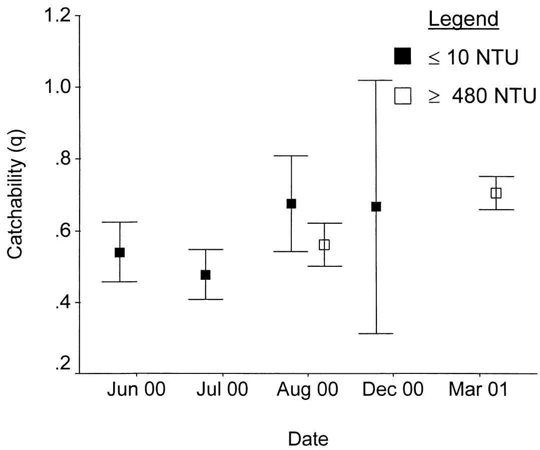

FIGURE 6.—Catchability coefficients of rainbow trout among sampling occasions and levels of turbidity (solid squares = observations in water with ≤10 nephelometric turbidity units [NTU]; open squares = observations in water with ≥480 NTU) in the Colorado River, Grand Canyon National Park, Arizona, during June 2000–March 2001. Vertical bars show 95% confidence intervals.

low at low fish density but rises because the fishing search rate increases with increased fish density (Hassell 1978). This did not occur in our study because drivers did not linger in areas where fish density was noticeably high. Also, catchability in type III curves eventually declines due to gear saturation or other mechanisms. Catchability of brown trout should decline beyond some level of fish density due to gear saturation, but results from rainbow trout indicate that saturation should not occur until fish density exceeds at least 0.18 fish/m^2. Such density did not occur in our study for either species, and the shape of the relationship between brown trout q and N_1 is obscured when density exceeds 0.025 fish/m^2.

The positive trend in the left-hand portion of the brown trout (q, N_1) curve must result from changes in fine-scale distribution of brown trout across low-to-intermediate density rather than some artifact of the fishing process. Brown trout are typically characterized as stationary, sometimes territorial fish with specific habitat preferences (Bachman 1984). They display preferences for discrete combinations of depth, velocity, and substrate, but the presence of other trout does not preclude brown trout from occupying such areas in high density (Bohlin 1977; Shirvell and Dungey 1983; Gatz et al. 1987). Crowding often results in expansions of brown trout aggregations into marginal habitats. Shirvell and Dungey (1983) noted a higher variance in brown trout depth preferenda during periods of high fish density. Similarly, Greenberg (1994) found that at low density, brown trout tended to use channel midsections, but at high density, many individuals were forced to use channel margins.

The expansion of local brown trout aggregations towards channel margins in the Colorado River may explain, in part, why a higher fraction were captured in areas of intermediate or high density than at low density. Higher catchability and higher density of brown trout over rocky shoreline types (ledges, cliff faces, bedrock, and cobble bars) probably enhances this effect. Brown trout are frequently associated with large, rocky substrates (Bachman 1984; Greenberg 1994), and density of electric fields (and thus, catchability) tends to be greater over such substrates (Reynolds 1996).

Catchability of rainbow trout was independent of fish density but was affected by turbidity, conductivity, and shoreline type. In contrast to brown trout, rainbow trout catchability was greater over sand–silt rather than rocky shoreline types, although the effect magnitude was much smaller than for brown trout. Regardless, these results suggest that interactions between fish density and habitat preference, shoreline type, and electrofishing catchability are complex and species-specific. Similarly, Bohlin and Sundstrom (1977) concluded that variation in catchability is attributable to fish behavior (especially territoriality) in relation to the environmental heterogeneity of the stream environment. Varying degrees of territoriality displayed by brown trout (Bachman 1984) and rainbow trout (Gatz et al. 1987) would thus be expected to produce different patterns in catchability when compared across habitat types and fish density.

Turbidity can affect electrofishing catchability through effects on netting efficiency, fish behavior, or both. Electrofishing catch rates tend to increase over low-to-intermediate levels of turbidity, and then decline over higher levels (Reynolds 1996). Moderate levels of turbidity apparently decrease the likelihood that fish will perceive and actively avoid the electrofishing boat before they are captured (Kirkland 1965), but stunned fish are more difficult to observe and net when turbidity levels are too high (Dewey 1992). Reduced light penetration caused by turbidity also alters trout behavior by reducing reactive distances, altering foraging behavior, and decreasing association with substrates (Noggle 1978; Gradall and Swenson 1982; Barrett et al. 1992). We hypothesize that turbidity levels observed during August 2000 and March 2001 concealed the boat from rainbow trout, yet were not high enough to conceal the fish from the netting crews.

Low water temperatures probably further reduced the ability of rainbow trout to avoid capture during turbid water periods. Turbid water catchability coefficients during August 2000 were not different from clear-water coefficients estimated from the same period, yet were collectively greater than coefficients estimated less than one month earlier. Temperature declined and turbidity increased during sampling occasions from July 2000 onward, and catchability of rainbow trout increased. Fish are less likely to avoid capture due to lowered metabolism at low water temperatures, although this effect can be offset by decreased flotation rates in cold water (Reynolds 1996; McInery and Cross 2000). Regardless, turbidity and temperature probably interact to affect the ability of fish to detect and avoid capture by electrofishing.

We found that the effects of conductivity on catchability of rainbow trout were confounded by temperature and turbidity. As a single covariate or in the presence of only temperature or turbidity, conductivity is not significantly related to catchability. Turbidity was always related to catchability regardless of which covariates were present or which procedure was utilized. Conductivity is often only weakly associated with variable electrofishing efficiency (Hill and Willis 1994; Dumont and Dennis 1997) and is probably of negligible importance below 1500 μS/cm (Serns 1982; Bayley and Austen 2002).

Management Implications

Conducting electrofishing surveys at night during discrete times of year can reduce bias in catchability, often because the influence of environmental variables or fish behavior are minimized at such times (Paragamian 1989; Dumont and Dennis 1997; McInery and Cross 2000). Our study demonstrates that despite diel standardization, electrofishing catchability can vary among fish density, fish species, and a host of seasonal and environmental factors. Bias in catchability can thus arise within a single sampling occasion if fish density or environmental gradients vary strongly across the study area. Environmental factors can affect catchability by influencing gear performance, fish behavior, or both. More complex interactions probably exist, such as when variations in fish density due to habitat preferences or territoriality interact with physical characteristics of microhabitats that may, in themselves, influence catchability.

Bias in catchability posed by uncontrolled variables (singly or in aggregate) in our study was measurable at stated probability levels, but may not be detrimental to interpretation of long-term CPUE trend data unless the magnitude of bias is indistinguishable from real changes in fish density across spatial and temporal scales of interest. However, even modestly variable catchability could seriously confound studies that require unbiased estimates of population or cohort size (i.e., bioenergetics or age-structured population models; Bayley and Austen 2002). Ideally, to ensure an accurate estimation of fish abundance and a valid interpretation of trends in fish population size as inferred through CPUE data, investigators should quantify bias in catchability due to biotic and abiotic factors (Peterman and Steer 1981; McInery and Cross 2000; Bayley and Austen 2002). The added costs of evaluating catchability over a range of conditions should ultimately outweigh the risks of misinterpreting CPUE data that is uncorrected for variable catchability (Bayley and Austen 2002), especially if critical management decisions affecting commercial fisheries (Peterman and Steer 1981) or endangered fish are based on such data. The costs of evaluating catchability can be minimized by periodically conducting experiments during routine field sampling over a range of conditions. At a minimum, CPUE data should be interpreted carefully and sources of bias in catchability should be recognized.

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